

NOTES ON A COLONY OF POLISTES FUSCATUS HUNTERI BEQUAERT

By HERMAN T. SPIETH

THE CITY COLLEGE OF NEW YORK AND THE AMERICAN
MUSEUM OF NATURAL HISTORY

The genus *Polistes* consists of a cosmopolitan group of social vespid wasps. Various observers have described the founding and maintenance of the polistine colonies. As information about the divers species accumulates, it is obvious that, while all the species follow the same broad basic pattern, there are many behavioral differences between species and perhaps between various populations of the same species. This is not surprising, especially when one considers the number of species and the vast geographical range of the genus. Just how diverse the pattern of activities of the genus will eventually prove to be can not be determined until many more observations have been made both on previously studied species and on those species which have not as yet been critically observed. So far as could be ascertained no records of the activities of *Polistes fuscatus hunteri* Bequaert have previously been made known. The following observations on this sub-species, although in no sense complete, are based on the data collected from a colony of *P. hunteri* Beq. during the summer of 1945 while the author was at Tyndall Field, Florida.

The nest under observation was located on the ceiling of the open porch of a small, single story house in Port Saint Joe, Florida. The porch faced south and the nest was placed in the northwest corner with the holdfast attached to the upper inner edge of a wooden, cavetto style molding. The house was approximately fifteen months old and had been occupied continuously since its completion. There seems to be adequate evidence that this was the first nest that *P. hunteri* had constructed on this porch. Another nest was found about fifty feet away in the shrubbery on the south side of a house of the same type and age on the adjoining lot. This shrubbery had been planted during the fall of 1944 so that the nest in it also seems to rep-

resent new colonization for the species. When the author moved into the house on 1 March, 1945, the nest on the porch was noted as a tiny comb but no observations were made until July 30. Once observations were started, they were continued daily (with the exception of five days from September 10 to 14) until October 7 and were made during the early morning and evening hours and on occasional off-duty days.

Although the nest was protected from the elements by the porch, it was easily accessible for observation. *Polistes fuscatus hunteri* Beq., is a gentle wasp and the constant presence and activity of human beings on the porch seemed to condition this particular colony to the presence of large animals. At any rate, the wasps seemed less excited by my presence than were those of the nest located in the shrubbery. The method of observation was to stand on a stool within close proximity to the comb. A thin metal mirror attached to a stick and slipped between the ceiling and the comb showed the top of the comb. By using a flashlight and the mirror, it was possible to count the number of individuals that slept on the comb. A porch light enabled one to make general observations at various times after darkness had fallen.

COLONY POPULATION

From July 30 to August 15, seven individuals worked and slept on the comb. All these were females and one, by virtue of her activity as well as her more worn appearance, was considered to be the foundress of the colony. During this time, no new individuals emerged. On August 15 two individuals emerged and that night nine specimens were counted. One female emerged on the 16th and another on the 18th, so that on the night of August 18 eleven wasps slept on the comb. During this period (July 30 to August 18) apparently there was no mortality among the adults. From then on, however, disparity constantly existed between the number that was expected and the actual number counted sleeping on the comb. It is true that apparently an occasional individual spent the night away from the comb, but the disparity was too great to be accounted for by this cause alone. From August 19 to September 6, at least thirteen individuals emerged, making a total of twenty-four wasps

that were expected in the population. On the night of September 6, fifteen individuals slept on the comb, thus leaving nine unaccounted for. During the next few days a number of individuals emerged. It was impossible to determine the exact number, but on September 9 twenty females slept on the comb and one on a morning glory vine nearby. From then on it was not possible to take an accurate census, due mainly to the appearance of males in the nest. It would seem that either mortality or desertion from the colony occurs as the season goes along. Considering the hazards that the wasps must face when foraging abroad for food and building materials, it is not surprising that some individuals should fail to return to the nest. The fact that seven individuals should have suffered no fatalities during the period from July 30 to August 18, inclusive, indicates that an adult *Polistes* is well able to care for herself in a hostile world.

As indicated above, no observations were made from September 10 to 14 inclusive (at which time I was on temporary duty at another Army post). During this period males appeared in the colony and became steadily more numerous from then on. Due to the hostility of the females toward the males, the latter were usually found on the top of the comb. At night they, plus some workers, slept on the top, packed so densely that it was impossible to count the exact number. It is certain, however, that the adult population at any one time never reached more than thirty and probably was less than twenty-five.

The "shrubby nest" (as we shall designate the previously mentioned nest located in the neighbors' shrubs fifty feet away) underwent a parallel development except that it was "younger" than the porch nest. At all times it was smaller and males did not appear until September 28. Unfortunately this nest was destroyed before it had completed its cycle.

THE COMB AND ITS CONSTRUCTION

On March 1 the comb consisted of several cells, probably not more than six. By August 3 there were forty-three cells and when the colony broke up on October 29 there were 146 cells. The final nest shape was asymmetrical, probably due to the loca-

tion of the nest in the corner of the porch. The shrubbery nest was symmetrical in construction. The porch nest was attached to the upper edge of the inner face of a concave cavetto style molding that ran around the porch ceiling with the holdfast itself adhered to the wooden molding and extended on up to the ceiling. By August the nest had grown to such a size that it filled the corner and thus new cells could be added on only two sides, viz., the east and south sides. The holdfast was strengthened and enlarged from time to time, and on August 26 it was observed that a secondary attachment had been made to the molding on the north side of the porch.

From time to time individuals were observed returning to the nest with a pellet of wood pulp of from 1 to 2 millimeters in diameter. This pellet, unlike the food balls, was carried and handled almost exclusively by the mouth parts, although once an individual was seen to use her fore legs while manipulating the wood pulp. Upon arrival at the nest, the wasp might either divide or give the entire pellet to other wasps or might retain the whole pellet herself. It was not possible to learn what determined which procedure was to be followed, but in any case the wood pulp pellet was ready for immediate use when brought into the nest. Without further ado, the wasp would run over the surface of the comb until she found a cell that suited her for further construction. She would then align her longitudinal axis with the wall of the cell and, moving backwards, spread the wood pulp over the edge of the cell. In doing this, the pulp was actually spread by the mandibles while the other mouth parts, except for the labrum, were used to support the pellet. At the same time the antennæ rapidly and continuously tapped the wall of the cell, one on either side. The antennæ always tapped that part of the cell that had been previously constructed. At first the pulp was rapidly and thickly spread over the edge of the cell wall, and then the wasp went over it again and again until it was thinned and smoothed to her satisfaction. Invariably she moved backwards as she worked with the wood pulp, but she might move either clockwise or counter-clockwise and often changed her direction several times during the addition of a pellet.

To the queen apparently belonged the task of initiating the construction of new cells. Since she apparently did not leave the comb during the period of observation, she always had to solicit the wood pulp necessary to build the new cells. A single pellet of pulp would furnish enough material to build a tiny shallow cell. While it was still damp, she would at once (or, very rarely, shortly thereafter) oviposit in this new cell. On August 29 the queen was observed to build a new cell, oviposit in it and then, after having very briefly cleaned herself and visited two larvæ, she approached a worker who was building on an older cell and not only demanded and received what was left of the pellet but also she re-collected what had been spread out. The queen then proceeded to select a site and start a new cell. It took her seven minutes to select the site for the new cell and six minutes to construct it. Having finished the cell she did not immediately oviposit. This, however, was the only time that she was not observed to oviposit immediately after completing the construction of a new cell.

The new cells were always added to the edge of the comb and were directed not downward but laterally. As the larvæ grew and the cells were enlarged, then the additions were so made that the opening of the mature cell faced downward. During the last two months of the colony's existence, the new cells were piled up on the edge of the comb so that the dorsal surface of the comb actually became concave. This shallow concavity was a favorite resting spot for the sentinels and males and at night was filled with sleeping individuals.

No more wood pulp was added to a new cell until the egg had hatched and the larva started growing. Then the workers kept constantly adding to the walls of the cell so that by the time the larva had reached maturity, the cell was large enough to accommodate the pupa. Not all cells were of exactly the same length and thus the stimuli that effected the construction of the cells seemed to be derived from the larva rather than from the surrounding cell walls. Different stimuli, however, affected the larva and if when it was ready to pupate its cell was shorter than were the surrounding ones, then it would add silken material until it brought the walls to the approximate level of the

surrounding cells. Having done this, it would then spin a rounded pupal cell cap. If the cell was as long as, or longer than, the surrounding cells, then the pupal cell cap was spun on the ends of the wood pulp walls and was flat rather than rounded.

When the adult emerged it perforated the pupal case by cutting a circular flap from the end of the pupal cell. This flap attached at one side hung downwards while the cut edges of the cell were always rough and ragged. The older workers would immediately refurbish the cell by scraping out the interior, removing the flap and leveling the ragged edges so that the cell wall was even with that of the surrounding cells. Quite different stimuli were obviously involved in refurbishing the cells from those involved in the original construction.

The materials collected during the refurbishing of the cells were not discarded but were chewed up into pulp and used for the construction of other cells. Thus the final comb although principally made up of wood pulp also contained material derived from the larval silk.

FOOD AND FLUID

The solid food utilized by the colony consisted of chunks of caterpillars. Apparently this did not include any part of the caterpillar digestive system but seemed to be made up of the body wall. These pieces varied considerably in size, an average piece being $3 \times 3 \times 3$ mm. Sometimes the pieces were very small, although occasionally they were so large that the individual was unable to make a proper landing on the nest. One such overloaded worker calmly flew across the porch, landed on a flat surface and clipped off a protruding piece from the chunk she had been carrying. Having done this, she was then able to land on the comb. At no time was an entire caterpillar brought to the comb; rather the food always consisted of pieces that had been cut from individuals. When flying the wasp carried the food by means of the mouth parts and the fore legs. When such an individual landed she supported herself by the meso- and meta-thoracic legs.

Invariably when the food bearer alighted on the nest, she was

accosted by one of the householders and then one of three things would happen: (1) The bearer might insist on retaining the food. If she insisted, she usually would succeed although she might have to refuse several applicants. (2) The entire food mass would be turned over to the applicant. (3) The food mass would be divided with another individual. The third procedure was most common and the division was accomplished by means of the mandibles and usually resulted in a rather equitable distribution of the food. Sometimes in the case of a large mass the applicant would receive the larger part and then this in turn might be divided with another nest-mate.

Once this division had been accomplished then the wasps would proceed to masticate each chunk and reduce it finally to a spherical bolus. Having started the process of mastication an individual would only rarely be molested by a nest-mate. Mastication was accomplished by the mouth parts aided by the antennæ and the fore legs. Only the tips of the fore tibia and the basal segments of the tarsi—not the tarsal claws or distal segment—came into contact with the food. Mastication did not appreciably decrease the size of the food mass and an adult was never observed to eat any of the food. After formation of the bolus, the wasp would then walk across the comb and finally select a larva which would then be offered the food. This was done by means of the mouth parts alone and the bolus, plus most of the head of the adult, was inserted into the larval cell. The larva would be allowed to feed for five to ten seconds and then the adult would retract her head and a large cavity could be seen on the side of the bolus where the larva had eaten away the food. The bolus would then be reformed, after which the adult might return to the same larva that she had been feeding or she might go on to another cell. Sometimes she would feed as many as three larvæ with one bolus. Exception to the normal procedure might occur with older larvæ to whom a small bolus of food might merely be given and then the adult would immediately remove her head and allow the larva to handle the food without aid. No reasons could be determined for the selection of the larvæ that received food. Sometimes an adult would visit many cells before she selected a larva to feed. Obviously there must have been some stimulus involved but it was not

apparent to the observer. Neither could any reason be determined why some larvæ might receive an entire bolus while another one would be given only a part of the available food.

Often individuals would return to the nest without any visible cargo. They would be accosted immediately by a nest-mate who would usually nudge the returnee, and then there would ensue a brisk tete-a-tete between the two individuals involving rapid mouth movements which probably accompanied the transfer of materials from the returnee to the applicant. Apparently the returnee had a supply of nectar or other substance that was sought by the applicant. If the tete-a-tete lasted for some time then the applicant, after having finished with the returnee, would hold a tete-a-tete with another householder. Now and then a wasp would return and refuse to cooperate with its mess-mates. Such individuals were often roughly handled by the householders. In such instances, if nudging and shoving did not produce results, the usual treatment was for the householder to seize with her jaws the dorsum of the returnee's abdomen in the region of the petiole. Then she would chew vigorously and with rare exceptions such treatment would quickly cause the returnees to acquiesce to the demands made upon them. All individuals that returned to the nests were accosted, but it seemed that those that carried no material externally, *i.e.*, meat or wood pulp, were sought most eagerly. When males appeared in the colony they would rush to accost those returnees that might be carrying nectar but strictly avoided those carrying meat or wood pulp. These activities between the adults seem to be best classed as examples of trophallaxis.

On two occasions when the humidity was obviously low (in each case a meteorological front had passed through the area just a few hours before), clear fluid was seen in all cells, *i.e.*, not only those that contained larvæ but also those in which eggs were present. This was placed on the walls of the cells in small droplets. Other than on these two occasions there was no sign of fluid per such being distributed to the developing individuals.

OTHER ACTIVITIES OF THE COLONY

One of the most characteristic features of the colony was the behavioral pattern followed by the individuals on the comb.

This consisted of periods of rest followed by surges of physical activity. If an individual returned from afield, she was invariably accosted by one or more nest mates. This activity would in turn stimulate all other individuals on the comb to activity and almost immediately all of them would be visiting larvæ, tete-a-teting with the returnee, moving about on the comb, or cleaning themselves. One by one, if no other stimulating incidents occurred, the individuals would relapse into a state of quiescence until all the individuals would be resting. Before the colony returned to a state of rest, every individual would have cleaned herself and have visited one or more, usually more, larvæ.

These periods of rest were of much longer duration than the periods of activity. While on the comb, the individual wasp unquestionably spent most of the time resting. After a trip afield an individual apparently always indulged in a prolonged rest before again returning to the field. A resting wasp assumed a characteristic posture with drooping antennæ, and with its body in contact with the comb.

Next to resting, the individual wasp spent most of her time cleaning herself. After activity of any sort, the individual invariably cleaned itself. The front legs were used to clean the face and associated structures such as the mouth parts and antennæ. The hind legs, assisted by abdominal movements, were used to clean the middle legs, abdomen and distal three-quarters of the wings. The top and rear of the head, the thorax and basal fourth of the wings were cleaned by the fore legs. Most often just the face and associated structures were cleaned, and least often the thorax and top of the head. The latter apparently was a gymnastic feat of some difficulty.

When an individual returned from afield, the surge of activity she created would continue until all materials, regardless of the type, that she had brought back had been disposed of. During periods of the day when the wasps were busily returning to the nest with food and wood pulp, then the colony was in an almost constant ferment of activity. At such times the population on the comb was small, but never was it deserted and usually five or more individuals were somewhere about. One or more of

these that remained on the nest was always on the top of the comb and seemed to serve as a sentinel; these individuals on the top invariably rested with their faces directed outward. If a strange being or object approached the nest they were the first to become alert. Their antennæ would be lifted, straightened, and directed forward, slightly upward and divergated at about 45 degrees. Their bodies would be raised from the comb and, if really alerted, they would also raise their wings in preparation for attack. Individuals on the under side of the comb might also assume the alert position but apparently those on the dorsal surface were the first and most easily stimulated.

If the colony had been quiet for a time and no intrusion from foreign objects or returnees had stimulated the individuals to activity, then suddenly one of the resting individuals would become active, either to clean itself, to move about preparatory to leaving the comb or most usually to visit the larvæ. Such activity would then stimulate the rest of the colony to activity. Thus either internal or external stimuli might start a cycle of activity. It is to be noted that if an individual had been afield, or had been working with wood pulp or meat, then she always cleaned herself both before and after visiting the larvæ. If she had been merely resting then she might visit the larvæ without cleaning herself. After the visit she would clean herself. The rule seemed to be that an individual cleaned herself after every phase of activity.

As stated above, during the surges of activity the wasps visited the larvæ. In such cases the wasp would move over the ventral surface of the comb, pausing momentarily at the various cells, select a cell in which a larva was present, insert her head and antennæ deeply (much further than when the wasps preferred food to the larvæ) and spend twenty to forty seconds with the larva. During this time the antennæ could be seen to vibrate gently. The wasp would visit from one to twenty larvæ in succession, but in doing so she might inspect many more without actually sticking her head into the cell. This activity was most characteristic and common and was interpreted as trophallaxis. No counts were made as to cumulative numbers of times that a single larva was visited during a day, but it certainly must have been many hundreds of times.

When the larvæ were ready to pupate they were ignored by the wasps and were neither fed nor visited for trophallactic exchange. Likewise the eggs and young larvæ were ignored. One of the unobserved features about the colony was how the very young larvæ were cared for. Apparently, until they were about one-fifth grown, the wasps completely ignored them with the exception of those rare instances when fluid was deposited in the cells. At that time all cells regardless of the presence or non-presence of an occupant received a portion. At no time (even though special attention was paid to this question) was a wasp observed to deal with any of those cells that contained eggs or young larvæ.

On those days when the ambient temperature was high, individual wasps were observed to raise their bodies from the comb and rapidly and vigorously beat the air with their wings. It was not possible to determine the significance of this activity. There seemed no relationship between the position of the wasp on the comb and the activity.

In cleaning herself, visiting the larvæ, resting, etc., the queen acted like all the wasps except that (1) she seemed to prefer the central area of the ventral surface of the comb as her resting and sleeping locale; (2) she quickly and easily drove all other wasps from this area, and (3) often she would violently shake herself much in the fashion that a dog shakes the water from its body after having been immersed. The queen was the only individual that indulged in this peculiar activity and no significance could be attached thereto.

OVIPOSITION

Oviposition was observed numerous times. In all cases observed, whether in a new cell or an old one that had been vacated by its previous inhabitant, the queen was the individual that produced the eggs. In the case of new cells she would, as shown above, build the cells from a single pellet of wood pulp and then oviposit in the cell while the walls were still damp. The ovipositing sequence was as follows: (1) As soon as she had finished a cell or discovered an empty one she would inspect it carefully, touching the inner surfaces with her antennæ; (2) she

would then turn about, insert her abdomen for a few seconds; (3) then remove her abdomen, change her position on the comb and re-insert the abdomen into the cell and proceed to oviposit.

During the actual period of oviposition the abdomen was arched slightly and for the first sixty seconds or so might be seen to move about and then become quiet. About four to five minutes were necessary for oviposition and the termination could be anticipated by the fact that the queen's antennæ began to vibrate for several seconds before she removed her abdomen from the cell. Having placed the egg in the cell she turned quickly and inspected it carefully with the tips of her antennæ. She then cleaned herself and visited some of the larvæ.

Oviposition took place at various times during the day and there seemed no definite time or rhythm involved, although it seemed restricted to the hours of daylight.

PUPATION AND EMERGENCE OF THE ADULT INDIVIDUALS

Mature larvæ pupated at all hours of the day and night. The spinning of the pupal cap took several hours. A larva would spin a small sector by wagging its head back and forth with a sidewise motion, then suddenly it would retract into the cell, rotate its body about one-fifth to one-third of a turn while retracted, extend itself and proceed to work on a new sector which invariably overlapped that area it had just completed.

When the adults of the shrubbery nest were destroyed, the comb itself was secured and the larvæ and pupæ removed for study. The full fed larvæ that had just spun their cocoons but had not shed the last larval exuviæ were located in the cocoons with their heads directed downwards, but individuals that had just shed this larval exuviæ (just transformed into exarate pupæ and were still unpigmented) had their heads directed upwards in the cells. Those individuals that were fully pigmented and ready to emerge had their heads directed downwards. Thus the individuals change direction at least twice after the cocoon has been spun. Probably the full fed larva, after it has finished the cocoon and when ready to pupate, is located so that its head is directed toward the top of the comb. The pupa therefore is similarly oriented. When the pharate stage of the adult is at-

tained, however, then the individual reverses its position in the cell and with its head directed downwards is ready to emerge.

Emergence of adults took place at all hours of the day and night. One individual was observed to emerge at 6.20 in the evening. She cut her way out, crawled out of the cell and onto the comb, cleaned her antennæ, visited the nearest larva, tete-a-teted with an adult, visited two other larvæ, cleaned her wings and hind legs, explored the comb, and then became quiescent.

In the meantime an adult had discovered the empty cell and became much excited. She cleared away the flap-like cap and the ragged edges, forming a ball of pulp from the material. Then she entered the cell and apparently scraped the inner walls with her mouth parts. She moved around on the comb but kept constantly returning to the empty cell and scraping the inside. This continued for at least fifteen minutes. The pellet of pulp which was derived from the cap and the scrapings was eventually built into a cell.

THE MALES

Sometime during the break in the daily observations that occurred between September 10 to 14, the males appeared in the colony. Because of their color and the shape of their antennæ, they could be readily identified. The females constantly drove the males from the ventral surface of the comb and perforce they spent most of their time on the top of the comb. They would, however, come down onto the ventral surface to visit the larvæ and to tete-a-tete with those females that returned to the colony without any visible cargo. They never approached a female that was bearing meat or wood pulp. They did, however, forage for themselves among the flowers in the neighborhood where they could be caught in considerable numbers.

During the remainder of the life of the colony the males became more and more abundant. Gradually the workers were less and less able to keep the males from almost monopolizing the ventral surface of the comb.

As stated above only the queen was observed actually to lay eggs. Since, however, these observations covered only a fraction of all the eggs actually laid, it is impossible to say that the

males were the offspring of the queen although circumstantial evidence indicates that such was the case in this colony.

BREAK-UP OF THE COLONY

On September 23 it was observed that several cells were empty and that apparently this was due to larval mortality since the larvæ that had occupied these cells had not been full-grown and certainly had not pupated. Except for continuing mortality of this type, the colony seemed to proceed normally from then until September 27. On that date it was observed that the workers were no longer cleaning up the cells from which adults were emerging. The new adults were apparently all males. On the morning of September 28, most of the larval cells were devoid of inhabitants. At 7.00 P.M., on the same day, all the larvæ as well as the eggs were gone from the nest and now only pupæ (29), males and females, remained. The day was overcast and showers had fallen. Just as darkness fell, a rain squall accompanied with considerable wind struck the area. At 8.30 P.M., after the storm had abated, the comb was inspected and found to be completely deserted by the wasps. Inspection of the porch showed numerous individuals, both males and females, resting on the wooden surfaces and on the morning glory vines that were supported by trellises.

From September 28 to October 7, wasps were occasionally seen on the comb but never more than two individuals at any given time. A few of the twenty-nine pupæ emerged, but once the nest was deserted by the adults, ants invaded it immediately (they had done so in great numbers by 8.30 P.M., on the night of September 28) and cut their way through the pupal cases and ate and killed the pupæ.

On October 7 the comb was removed except for the basal part of the holdfast. From then until November 1, an occasional wasp would spend the night sleeping on the holdfast.

ENEMIES

The chief enemies of these wasps appeared to be various species of ants. Constantly the wasps drove the ants away and as long as an adult was about the comb, the ants were never able

to gain access to the colony. An attempt was made to transfer to another corner of the porch a colony of *Polistes fuscatus bellicosus* Cresson¹ which had to be destroyed from its original site. The adults of this colony, although transferred with the comb, immediately left the comb and returned to the old site. Ants invaded this comb within fifteen minutes of the time it was deserted.

Parasites also attacked the colony, although the actual invasion was never observed. As stated above, observations were not made from September 10 to 14 and when observations were resumed on September 15 it was noted that many of the cells in the central region of the comb had a silken, sheet-like structure running obliquely from the mouth of the cell into the interior. It was not possible to determine just what parasite was responsible for this condition. This sheet was not removed from the cell and, even though the volume of the cell was greatly reduced by its presence, nonetheless eggs were laid in these cells, presumably by the queen.

¹ It is obviously erroneous to consider *bellicosus* Cresson and *hunteri* Beq. as subspecies of *fuscatus*. They were both living in the same area and clearly not interbreeding. They are quite distinct in many ways and by all known criteria belong to different species. Despite this, since I am not familiar with the taxonomy of *Polistes*, I am following the present but incorrect nomenclature.